

University of Groningen

Prenatal light exposure affects early feather-pecking behaviour in the domestic chick

Riedstra, B.; Groothuis, T.G.G.

Published in:
Animal Behavior

DOI:
[10.1016/j.anbehav.2003.10.009](https://doi.org/10.1016/j.anbehav.2003.10.009)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2004

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Riedstra, B., & Groothuis, T. G. G. (2004). Prenatal light exposure affects early feather-pecking behaviour in the domestic chick. *Animal Behavior*, 67(6), 1037-1042. <https://doi.org/10.1016/j.anbehav.2003.10.009>

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

Prenatal light exposure affects early feather-pecking behaviour in the domestic chick

B. RIEDSTRA & T. G. G. GROOTHUIS

Zoological Laboratory, Department of Animal Behaviour, University of Groningen

(Received 7 March 2003; initial acceptance 28 April 2003;
final acceptance 7 October 2003; MS. number: 7640)

Recently we proposed that early feather pecking is a form of social exploration. Social recognition, important for exploration, is a lateralized function in the domestic chick. Lateralization of functions can be influenced by light exposure late in embryonic development. Therefore, we investigated whether this light exposure affected early posthatching feather-pecking behaviour in domestic chicks, *Gallus gallus domesticus*. White leghorn embryos either were exposed to light or remained in darkness in the last week of incubation. After hatching, they were housed in groups of two light-exposed and two dark-incubated chicks. Light-exposed chicks showed more feather pecking than did their dark-incubated cagemates. Dark-incubated chicks preferred to direct feather pecks to unfamiliar peers than to familiar peers; light-exposed chicks showed no preference. These effects were present in the first week after hatching and remained at least another 3 weeks. These results support the hypothesis that early gentle feather pecking is part of the normal behavioural repertoire of young chicks and influences social exploration. We discuss a possible mechanism underlying these results. We also suggest that it may be worthwhile not to expose embryos to light during the last week of incubation when housing hatchlings in commercial conditions, where feather pecking is a serious problem.

© 2004 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Feather pecking is a problem behaviour that occurs in virtually all commercially housed birds. Feather pecking includes both pecking at and pulling out feathers of group-mates. It causes economic losses through increased feed intake caused by loss of insulating capacity (Tauson & Svensson 1980), decreased egg production (Johnsen et al. 1998) and increased mortality (Blokhuys & Wiepkema 1998). Furthermore, feather pecking is generally regarded as detrimental to the welfare of recipients and signalling impaired welfare of the peckers (Blokhuys & Wiepkema 1998).

There are two major hypotheses about the cause of feather pecking. In both hypotheses, feather pecking is a redirected form of ground pecking (Savory 1995). The main motivational system underlying this redirection is either the food search system (Blokhuys 1989) or the dustbathing system (Vestergaard 1994). We have argued that early forms of feather pecking may not be controlled by either of these motivational systems proposing instead that early feather pecking is part of the chicks' normal

social behavioural repertoire and influences social exploration (Riedstra & Groothuis 2002). This hypothesis was based on the finding that chicks performed more feather pecking towards unfamiliar than familiar peers, and introduction of unknown chicks considerably stimulated feather pecking (Riedstra & Groothuis 2002; B. Riedstra & T. G. G. Groothuis, unpublished data).

Young domestic chicks are able to discriminate between unfamiliar and familiar individuals after only brief social experience (Zajonc et al. 1975). A prerequisite for chicks to become familiar with other individuals is the opportunity to explore others by pecking them (Zajonc et al. 1975). The ability to discriminate between familiar and unfamiliar individuals (social recognition) is a lateralized function, i.e. controlled predominantly by one hemisphere of the brain, in this case the right one (Vallortigara & Andrew 1991, 1994; Vallortigara 1992; Rogers 1995; Deng & Rogers 2002). Lateralization of the visual projections can be influenced by exposing embryos to light in the last few days before hatching. Birds have complete optical decussation, and the majority of birds preparing to hatch turn in the egg so that the right but not the left eye can receive light input (Oppenheim 1973; Rogers 1995). If the eggs are then exposed to light, the projections from the right eye to the nucleus geniculatus lateralis pars dorsalis and subsequent projections to the forebrain develop more

Correspondence: B. Riedstra, Zetveld 95, 8447BB, Heerenveen, The Netherlands (email: Bernd.Riedstra@wanadoo.nl). T. G. G. Groothuis is at the Zoological Laboratory, Department of Animal Behaviour, University of Groningen, Kerklaan 30, 9750 AA, P.O. Box 14 Haren, The Netherlands.

strongly than do the projections from the left eye (Rogers 1996; Rogers & Deng 1999; Koshiba et al. 2002). These projections do not occur when chicks are incubated in complete darkness.

Light illuminating the right eye of an embryo stimulates the growth of the projections from the right eye to the left hemisphere, but social recognition is controlled by the right hemisphere (Deng & Rogers 2002). If social recognition is involved in feather-pecking behaviour, then light-exposed embryos are expected to perform worse in social discrimination by feather pecking later in life than are dark-incubated chicks, because in light-exposed chicks, left-hemisphere functions may be better developed than right-hemisphere functions and may dominate behavioural output. Light-exposed embryos are also more fearful early after hatching than are dark-incubated chicks (Dimond 1968; Rogers & Workman 1989). Increased fear is implicated in feather-pecking behaviour (Vestergaard et al. 1993; Jones et al. 1995); therefore, we hypothesized that embryonic exposure to light enhances the rate of early feather-pecking behaviour.

To study the effects of light on the frequency and social orientation of feather pecking, we exposed embryos to light or darkness and recorded feather-pecking behaviour in two conditions: where chicks were housed only with familiar conspecifics and where they were housed with both familiar and unfamiliar conspecifics.

METHODS

Experiment 1: Treatment with a Single Pulse of Light

Housing and treatment

We collected eggs of white leghorns that had been kept in large outdoor aviaries and placed them in a horizontal position in an incubator at the Zoological Laboratory of the University of Groningen. Eggs were collected randomly with respect to hen and laying sequence. The incubator was sealed such that no environmental light could penetrate when the door was closed. The eggs were incubated at 37.5°C and a relative humidity of 60%, and were turned automatically three times a day. After 7 days, the eggs were candled and removed if we detected improper development. Eighteen days after the onset of incubation, eggs were placed, in the dark, in two hatching trays at the same level in the same incubator. On day 19, after the onset of incubation, half of the eggs (embryos) in the incubator received a 2-h light pulse starting at 1500 hours from a 100-W incandescent light bulb approximately 50 cm above the eggs. Light intensities at the egg level ranged from 750 lx at the edges of the tray to 1000 lx directly under the light bulb. This treatment suffices to achieve enhanced lateralized growth of the visual projections (Rogers 1995). The remaining eggs in the incubator were covered so as to remain in darkness for the same period. After this treatment, all eggs were left to hatch in darkness. On the last day of incubation, we increased relative humidity to 80–85%. On the day of hatching, we removed chicks from the incubator in darkness in groups

of four. In each group, two chicks had received the light pulse (L-chicks) and two were dark-incubated chicks (D-chicks). Chicks were individually colour-marked with a blue or black felt-tipped nontoxic marker on the neck or head. Colours were alternated between groups. We created 19 groups in two hatches several weeks apart (10 groups in the first hatch) and housed groups in identical cages (0.9×0.75 m and 0.9 m high). Chicks housed in adjacent cages were fully separated from each other both visually and tactilely by the metal walls of the cages. Heat was provided by a 125-W porcelain heat bulb in each cage. The cage floors were covered with shredded hemp stalks. Water and food (DfK Chick Crumbs 2, Hendrix UTD, Boxmeer, The Netherlands) were provided *ad libitum*.

Observations

We recorded feather pecking 7, 14, and 21 days after hatching. All groups were observed during each of these days in four to six sessions, each lasting 15 min (13 sessions for each cage in the first hatch, 18 sessions for each cage in the second hatch). In each cage, we simultaneously recorded the number of feather pecks from each bird. Recordings were made by an observer standing in front of a cage speaking into a tape recorder, fully visible to the chicks. Twenty-six days after hatching, chicks were reallocated to new groups in the following way: the four D-chicks from two adjacent cages were housed together in a new but identical cage, and the four L-chick groups were similarly matched and housed in a different new cage. All 18 groups remained in this condition for 30 min. Chicks from the second hatch were placed back into their original cages after these 30 min and the experiment was terminated. The 10 newly formed groups of the first hatch remained in this condition for 3 days, after which the experiment was ended. We recorded feather-pecking behaviour for 30 min starting at four different points in these newly formed groups: 0 h after formation of the new groups in 18 groups, and 5, 72 and 76 h in 10 groups. We recorded feather pecking as before, but now we also recorded which individual was targeted by a feather-pecking bird.

Experiment 2: Double Light Pulse Treatment

Housing and treatment

Eggs of white leghorns obtained from a commercial poultry farm were treated similarly as the eggs in experiment 1, except that L-chicks received a 2-h light pulse twice: one on day 19 after the onset of incubation (starting at 1500 hours) and a second pulse 24 h later. Treatment and housing after hatching were as in experiment 1. We created 12 groups from one hatch.

Chicks were subjected to a social exploration test 4 days after hatching. The experimental set-up was as follows: in each cage we created two pairs, each consisting of one L-chick and one D-chick; then one pair from cage X was rehoused in a new cage with one pair from cage Y, and the second pair from cage X was rehoused with the second pair from cage Y.

Observations

Feather-pecking behaviour (frequency and social orientation) was recorded for 30 min directly following rehousing and confrontation with unfamiliar chicks. The chicks were then placed back into their original cages. On day 7 after hatching, we recorded feather-pecking behaviour in the home cage in four sessions of 15 min, as in experiment 1. Afterwards, the chicks were removed to one large group and the experiment was terminated.

Data Analysis

Feather-pecking rates and proportions were not normally distributed; therefore, we used only nonparametric statistical methods. All rates of feather pecking are expressed as the median number and range of pecks per bird per 15 min (Table 1 shows the mean \pm SE of the number of pecks per 15 min). Social orientation was defined as the proportion of the total feather pecks targeted at a familiar chick. In both experiments, the statistical unit for testing the effect of treatment on feather pecking was the home cage ($N = 19$ and $N = 12$, respectively). To record the social orientation of feather pecking, birds were reallocated to new groups in a pairwise manner. In experiment 1, the statistical unit in the social orientation condition to test for differences in feather-pecking behaviour was the newly formed group ($N = 9$). In experiment 2, the statistical unit in the social orientation condition for the rate of feather pecking was the pair of newly formed groups ($N = 6$, because every newly formed group had one duplicate). We used Wilcoxon signed-ranks tests to evaluate the effect of treatment on the rates of feather pecking and the social orientation within pairs of L-chicks and D-chicks. We also used the Wilcoxon signed-ranks test to assess whether social orientation deviated from random (1/3). All associations were calculated using the Spearman rank correlation. Statistical analyses were performed using SPSS 11.0 (SPSS Inc., Chicago, U.S.A.). All P values presented are two tailed.

Ethical Note

Feather pecking during the first few weeks after hatching is virtually never harmful to the individual pecked, nor is it an obvious expression of a compromised state of well being of the pecker. This early feather pecking is usually classified as mild or gentle feather pecking (Vestergaard et al. 1993; Bilčík & Keeling 1999). In contrast to pecking

later in life, where birds try to pull out feathers of conspecifics (severe feather pecking), it causes no distress, feather loss, skin lesions, blood loss or mortality. Feather pecking in our study was almost exclusively pecking without pulling at feathers and was therefore categorized as gentle. Throughout the text the adjective 'gentle' is implicit and will be omitted.

There was no sign that the colour marks on the plumage attracted pecks. Birds were checked twice a day on weekdays and once a day on weekends for general health and nutritional needs. Recovery cages, antiseptic antifeather-pecking spray and expert help were available at all times but never had to be used. All experiments were carried out under licence of the animal experiments committee of the University of Groningen. We found no detrimental effects of our experiment on the welfare of the chicks. At the end of the experiment, all chicks were donated to private persons.

RESULTS

Rate of Feather Pecking in the Home Cage

Experiment 1

Rates of feather pecking averaged over the 3 observation days of L-chicks and D-chicks in the same cage (Fig. 1) were positively associated (Spearman rank correlation: $r_s = 0.68$, $N = 19$, $P = 0.002$). Rates of feather pecking were significantly higher in L-chicks than in D-chicks (Wilcoxon signed-ranks test: $Z = -2.978$, $N = 19$, $P = 0.003$; Fig. 1). L-chicks already had higher rates of feather pecking than did their cagemates on the first observation day and persisted in having higher rates on the 2 subsequent observation days (Table 1).

Experiment 2

Rates of feather pecking between L-chicks and D-chicks in the same cage were positively correlated (Spearman rank correlation: $r_s = 0.67$, $N = 12$, $P = 0.020$). At 7 days posthatching, L-chicks had higher rates of feather pecking than did D-chicks (Wilcoxon signed-ranks test: $T = 0$, $N = 12$, $P = 0.002$; Fig. 2).

Social Orientation of Feather Pecking

Experiment 1

During the first 30 min after rehousing, the rate of feather pecking of the L-chicks did not differ from that of

Table 1. Median (and range) and mean \pm SE number of feather pecks in the home cage in experiment 1

Days after hatching	Median		Mean		Z	P
	Light	Dark	Light	Dark		
7	5.0 (1.1–35.9)	3.2 (0.9–18.0)	4.4 \pm 0.98	8.0 \pm 1.91	–2.053	0.040
14	6.1 (1.1–37.8)	2.8 (0.5–50.1)	5.4 \pm 2.52	10.5 \pm 2.62	–2.596	0.009
21	6.3 (0.6–296.5)	3.1 (0.5–47.8)	12.0 \pm 3.66	36.8 \pm 16.43	–2.254	0.024

Rates are expressed per bird per 15 min ($N = 19$) for light-incubated chicks and dark-incubated chicks for each of the 3 observation days separately (Wilcoxon signed-ranks test).

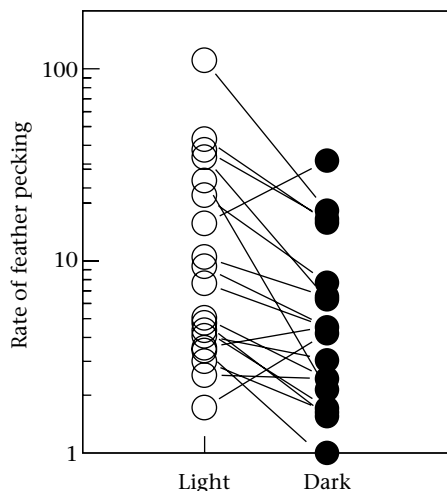


Figure 1. Within-cage comparison of the average rates of feather pecking (pecks per 15 min per bird) in light-incubated chicks and dark-incubated chicks in experiment 1, calculated over the 3 observation days (logarithmic scale). Lines connect light-incubated chicks (○) and dark-incubated chicks (●) housed in the same cage.

the D-chicks (Wilcoxon signed-ranks test: $T = 12.0$, $N = 9$, $P = 0.214$). The proportion of feather pecks by D-chicks aimed at the familiar individual was lower than that by their former (light-exposed) cagemates ($T = 2.0$, $N = 9$, $P = 0.025$; Fig. 3). The proportion of pecks at the familiar bird was lower than expected if cagemates had been randomly targeted (expectation = $1/3$) in the D-chicks ($T = 0$, $N = 9$, $P = 0.007$), but did not deviate from random in the L-chicks ($T = 9.0$, $N = 9$, $P = 0.110$). There were no significant correlations in either L- or D-chicks between the proportion of pecks given to the familiar chick in the first 30 min after rehousing and rates of feather pecking expressed in the home cage or in the rehousing condition during the same 30 min (Spearman rank correlation: $r_s = -0.41$ to 0.50 , $N = 9$, all P values > 0.160).

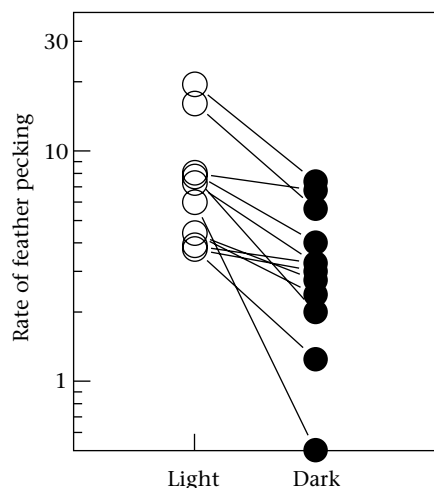


Figure 2. Within-cage comparison of the difference in rates of feather pecking between light-incubated chicks and dark-incubated chicks in experiment 2 (logarithmic scale). Lines connect light-incubated chicks (○) and dark-incubated chicks (●) housed in the same cage.

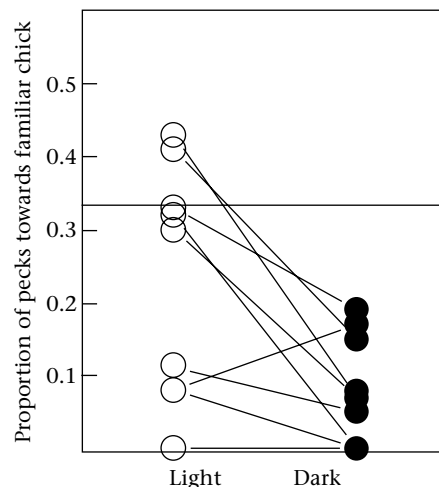


Figure 3. Social orientation of feather pecking in experiment 1 expressed as the proportion of total feather pecks aimed at the familiar chick. Lines connect paired light-incubated chicks (○) and dark-incubated chicks (●). Horizontal line ($Y = 1/3$) represents predicted proportion when pecks are evenly distributed between unfamiliar and familiar conspecifics.

In the 10 groups of the first hatch that remained in their newly formed groups for 3 days, there were no significant differences in the rates of feather pecking between L- and D-chicks (Wilcoxon signed-ranks test: $N = 5$, all P values > 0.5) except 76 h after reallocation (median, L-chicks: 32.5, range 3.0–83.6; D-chicks: 3.8, range 1.3–53.5, Wilcoxon signed-ranks test: $T = 0$, $N = 5$, $P = 0.043$). There were also no differences in social orientation between the L- and the D-chicks at 5, 72 and 76 h after forming the new groups, nor did the orientation deviate from $1/3$ (Wilcoxon signed-ranks test: $N = 5$, all P values > 0.138).

Experiment 2

During the first 30 min after reallocation 4 days after hatching, the rate of feather pecking in the L-chicks did not differ from that in the D-chicks (Wilcoxon signed-ranks test: $T = 7.5$, $N = 6$, $P = 0.527$). The proportion of feather pecks aimed at the familiar individual by D-chicks did not differ from that of former (light-exposed) cagemates ($T = 4.0$, $N = 6$, $P = 0.173$; Fig. 4). Again as in experiment 1, the proportion of feather pecks to the familiar bird was lower than expected if cagemates had been randomly targeted in the D-chicks ($T = 1.0$, $N = 6$, $P = 0.046$), but did not deviate from random in the L-chicks ($T = 10.0$, $N = 6$, $P = 0.917$). We detected no significant correlation in either the L-chicks or the D-chicks between the rate of feather pecking on day 7 and either the rate or social orientation of feather pecking on day 4 (Spearman rank correlation: $r_s = -0.15$ to 0.39 , $N = 12$, all P values > 0.210).

DISCUSSION

We found a long-lasting effect of light exposure late in embryonic development on both the rate and the social

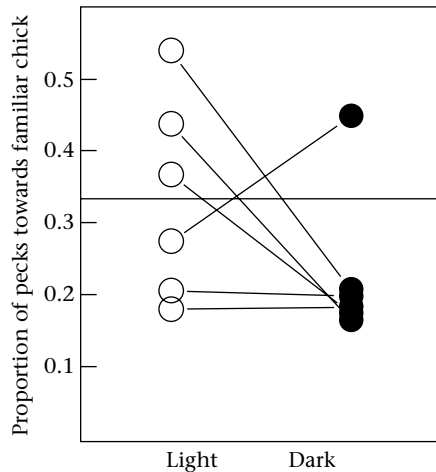


Figure 4. Social orientation of feather pecking in experiment 2 expressed as the proportion of total feather pecks aimed at the familiar chick. Lines connect paired light-incubated chicks (○) and dark-incubated chicks (●). Horizontal line shows predicted proportion when pecks are evenly distributed between familiar and unfamiliar conspecifics.

orientation of feather pecking in domestic chicks. Chicks exposed to light as developing embryos had higher rates of feather pecking in their home cages than did dark-incubated chicks. This was not the case when we assessed the social orientation of feather pecking directly after placing chicks in a condition where they were confronted with unfamiliar peers. The lack of differences in this condition may have been caused by the novelty of the condition, because, over time, the frequency of feather pecking in L-chicks again started to deviate from that of the D-chicks.

In contrast to dark-incubated chicks, light-exposed chicks showed no significant preference for targeting unfamiliar over familiar conspecifics when placed in a simultaneous two-choice condition. These effects were already present in the first week after hatching and may be long lasting, because in a slightly different set-up (experiment 1), this result was also obtained in chicks that were 3 weeks old. The dark-incubated chicks' preference for pecking unfamiliar peers disappears with increasing time after confrontation, suggesting that birds become familiarized through pecking (Zajonc et al. 1975).

At the treatment level, we conclude that birds that discriminate between familiar and unfamiliar birds by feather pecking in a social discrimination task have low rates of feather pecking in the home cage condition, and vice versa. These findings therefore support our hypothesis that early feather pecking is associated with social exploration (Riedstra & Groothuis 2002) and can be modified by early light exposure, which affects social recognition.

Lateralization

Light exposure before hatching influences the direction of lateralization of morphological structures and behavioural functions (Rogers & Workman 1989; Rogers 1995; Manns & Güntürkün 1999; Rogers & Deng 1999; Koshiba et al. 2002). Embryonic light exposure determines, for

example, in which hemisphere recall of imprinting memory becomes dominant (determined by obligatory use of the left eye/right hemisphere or right eye/left hemisphere system in specific tasks; Johnston & Rogers 1999). When embryos are not exposed to light, lateralization of behavioural functions will be established, but which hemisphere will be dominant in certain functions is not predictable (Rogers 1995). However, not all directions of lateralized behavioural functions can be influenced by light exposure. Light exposure does not affect the left eye preference for viewing a familiar social partner (McKenzie et al. 1998), or the preference for viewing conspecifics with the left lateral visual field before pecking at them (Vallortigara et al. 2001). Deng & Rogers (2002) found that lateralization of individual recognition or choice behaviour was not influenced by light experience before hatching. The authors used a set-up where chicks had to choose between a familiar and an unfamiliar conspecific in a runway. In such a set-up, chicks have to use the left eye to make a choice (Vallortigara & Andrew 1991). In a social-pecking test, the choice is to direct pecks preferentially at an unfamiliar chick (Vallortigara 1992), which is the general preference for chicks when both eyes are in use (Zajonc et al. 1975; Vallortigara 1992; Riedstra & Groothuis 2002).

In our study, D-chicks preferentially directed feather pecks towards the unfamiliar chick. The L-chicks showed no such preference, and the rates of feather pecking in that condition were similar. Assuming that individual recognition was located in the right hemisphere and was accessible to both L- and D-chicks, this lack of a preference may have been caused by a restriction in interhemispheric transformation of information (Nottelmann et al. 2002) or an overall dominance by the left hemisphere for behavioural output. If the ability to discriminate between individuals were hampered, then this may explain the increased pecking rates in the home cage: L-chicks may have been constantly trying to reacquaint themselves with their social environment.

Practical Implications

There are no reports on how much light chicken embryos receive under natural conditions during the sensitive period for light-induced lateralization. The minimum exposure needed to establish functional lateralization is also unknown (Rogers 1995). Hatcheries frequently expose embryos to light during the sensitive period, that is, the last week of incubation. Although feather pecking at early ages is almost exclusively gentle in form (Bilčík & Keeling 1999) and consequence (early feather pecking does not directly result in feather loss or lead to aversive reactions of the recipients), it may be worthwhile not to expose eggs to light during the last week of incubation for several reasons. First, frequent early feather pecking may result in plumage damage (Leonard et al. 1995; B. Riedstra, personal observation) which may give positive feedback to this behaviour because of the enhanced stimulus properties of damaged feathers (McAdie & Keeling 2000), potentially leading to even more damage. Second, early

gentle feather-pecking behaviour may turn into excessive gentle feather pecking that resembles a stereotypy (McAdie & Keeling 2002); both the process leading to the formation of a stereotypy as well as a stereotypy itself are generally regarded as signs of lower animal welfare (Mason 1991a, b). Third, feather-pecking behaviour is socially transmittable (Zeltner et al. 2000). Introducing frequent feather peckers into a group increases feather-pecking behaviour in infrequent feather peckers (Zeltner et al. 2000), which may have influenced our study because of the strong association between rates of pecking within cages between chicks of the two treatments. Finally, increased gentle feather pecking may develop into more severe forms of feather pecking, which clearly reduces the welfare of the recipients (McAdie & Keeling 2002; B. Riedstra & T. G. G. Groothuis, unpublished data).

Acknowledgments

We thank S. Daan, E. Erberfeld, A. Faber, R. Veenstra-Wiegman, S. Veenstra and M. Verweij for their help during this study. B.R. was supported by NWO grant 805-46.053.

References

- Bilčík, B. & Keeling, L. J. 1999. Changes in feather condition in relation to feather pecking and aggressive behaviour in laying hens. *British Poultry Science*, **40**, 444–451.
- Blokhuys, H. J. 1989. The development and causation of feather pecking in the domestic fowl. Ph.D. thesis, University of Wageningen.
- Blokhuys, H. J. & Wiepkema, P. R. 1998. Studies of feather pecking in poultry. *Veterinary Quarterly*, **20**, 6–9.
- Deng, C. & Rogers, L. J. 2002. Social recognition and approach in the chick: lateralization and effects of visual experience. *Animal Behaviour*, **63**, 697–706.
- Dimond, S. J. 1968. Effects of photic stimulation before hatching on the development of fear in chicks. *Journal of Comparative and Physiological Psychology*, **65**, 320–324.
- Johnsen, P. F., Vestergaard, K. S. & Norgaard-Nielsen, G. 1998. Influence of early rearing conditions on the development of feather pecking and cannibalism in domestic fowl. *Applied Animal Behaviour Science*, **60**, 25–41.
- Johnston, A. N. B. & Rogers, L. J. 1999. Light exposure of chick embryo influences lateralized recall of imprinting memory. *Behavioural Neuroscience*, **113**, 1267–1273.
- Jones, R. B., Blokhuys, H. J. & Beuving, G. 1995. Open-field and tonic immobility responses in domestic chicks of two genetic lines differing in their propensity to feather peck. *British Poultry Science*, **36**, 525–530.
- Koshiba, M., Kikuchi, T., Yohda, M. & Nakamura, S. 2002. Inversion of the anatomical lateralization of chick thalamofugal visual pathway by light experience. *Neuroscience Letters*, **318**, 113–116.
- Leonard, M. L., Horn, A. G. & Fairfull, R. W. 1995. Correlates and consequences of allopecking in White Leghorn chicks. *Applied Animal Behaviour Science*, **43**, 17–26.
- McAdie, T. M. & Keeling, L. J. 2000. Effect of manipulating feathers on laying hens on the incidence of feather pecking and laying hens. *Applied Animal Behaviour Science*, **68**, 215–229.
- McAdie, T. M. & Keeling, L. J. 2002. The social transmission of feather pecking in laying hens: effects of environment and age. *Applied Animal Behaviour Science*, **75**, 147–159.
- McKenzie, R., Andrew, R. J. & Jones, R. B. 1998. Lateralization in chicks and hens: new evidence for control of response by the right eye system. *Neuropsychologia*, **36**, 51–58.
- Manns, M. & Güntürkün, O. 1999. Monocular deprivation alters the direction of functional and morphological asymmetries in the pigeon's (*Columba livia*) visual system. *Behavioural Neuroscience*, **113**, 1257–1266.
- Mason, G. J. 1991a. Stereotypies: a critical review. *Animal Behaviour*, **41**, 1015–1037.
- Mason, G. J. 1991b. Stereotypies and suffering. *Behavioural Processes*, **25**, 103–115.
- Nottelmann, F., Wohlschlager, A. & Güntürkün, O. 2002. Unihemispheric memory in pigeons-knowledge, the left hemisphere is reluctant to share. *Behavioural Brain Research*, **133**, 309–315.
- Oppenheim, R. W. 1973. Prehatching and hatching behaviour: a comparative and physiological consideration. In: *Behavioural Embryology*. Vol. 1 (Ed. by G. Gottlieb), pp. 163–244. New York: Academic Press.
- Riedstra, B. & Groothuis, T. G. G. 2002. Early feather pecking as a form of social exploration: the effect of group stability on feather pecking and tonic immobility in domestic chicks. *Applied Animal Behaviour Science*, **77**, 127–138.
- Rogers, L. J. 1995. *Development of Brain and Behaviour in the Chicken*. Wallingford: CABI.
- Rogers, L. J. 1996. Behavioral, structural and neurochemical asymmetries in the avian brain: a model system for studying visual development and processing. *Neuroscience and Biobehavioral Reviews*, **20**, 487–503.
- Rogers, L. J. & Deng, C. 1999. Light experience and lateralization of the two visual pathways in the chick. *Behavioural Brain Research*, **98**, 277–287.
- Rogers, L. J. & Workman, L. 1989. Light exposure during incubation affects competitive behaviour in domestic chicks. *Applied Animal Behaviour Science*, **23**, 187–198.
- Savory, C. J. 1995. Feather pecking and cannibalism. *World's Poultry Science Journal*, **51**, 215–219.
- Tauson, R. A. & Svensson, S. A. 1980. Influence of plumage condition on the hen's feed requirement. *Swedish Journal of Agricultural Research*, **10**, 35–39.
- Vallortigara, G. 1992. Right hemisphere advantage for social recognition in the chick. *Neuropsychologia*, **30**, 761–768.
- Vallortigara, G. & Andrew, R. J. 1991. Lateralization of response by chicks to change in a model partner. *Animal Behaviour*, **41**, 187–194.
- Vallortigara, G. & Andrew, R. J. 1994. Differential involvement of right and left hemisphere in individual recognition in the domestic chick. *Behavioural Processes*, **33**, 41–58.
- Vallortigara, G., Cozzutti, C., Tommasi, L. & Rogers, L. J. 2001. How birds use their eyes: opposite left–right specialization for the lateral and frontal visual hemifield in the domestic chick. *Current Biology*, **11**, 29–33.
- Vestergaard, K. S. 1994. Dustbathing and its relation to feather pecking in fowl: motivational and developmental aspects. Ph.D. thesis, Royal Veterinary and Agricultural University, Copenhagen.
- Vestergaard, K. S., Kruijt, J. P. & Hogan, J. A. 1993. Feather pecking and chronic fear in groups of red jungle fowl: their relations to dustbathing, rearing environment and social status. *Animal Behaviour*, **45**, 1127–1140.
- Zajonc, R. B., Wilson, W. R. & Rajecki, D. W. 1975. Affiliation and social discrimination produced by brief exposure in day-old domestic chicks. *Animal Behaviour*, **23**, 131–138.
- Zeltner, E., Klein, T. & Huber-Eicher, B. 2000. Is there social transmission of feather pecking in groups of laying hen chicks? *Animal Behaviour*, **60**, 211–216.